14.

The Schooling Behavior of Mackerel: A Preliminary Experimental Analysis.

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(Plate I).

INTRODUCTION.

As indicated in the comprehensive review of the field by Allee (1931), animal aggregations and their significance have attracted increasing critical analysis in recent years. Curiously, the fish school—one of the most striking examples of well-integrated animal aggregations — has received remarkably meager critical attention. Spooner (1931) and Breder & Nigrelli (1935), considering various aspects of schooling in fishes, have noted this unfortunate lack of literature. Some notes on the schooling behavior of the herring, *Clupea harengus* L., by Newman (1876), constitute one of the earliest publications in this field. Nevertheless, Parr (1927) after a fifty year interval had a virtually clear field for his theoretical analysis of the schooling behavior of mackerel.

Fishes which do not school and have no visible aggregating tendency have been considered "non-social" forms. However, it is unwise to so classify a form which manifests no obvious social tendencies. Statistical evidence has demonstrated that the goldfish, which had been summarily thus dismissed, manifested a definite group effect; isolated individuals were found to have a higher rate of locomotor activity and oxygen consumption than did grouped goldfishes (Schuett, 1934; Escobar, Minahan & Shaw, 1936; Breder & Nigrelli, 1938; Shlaifer, 1938). Hence, social tendencies may be relatively obscure and not readily determined by casual observation.

At the extremes, it is a relatively simple matter to differentiate between a loosely aggregating fish and a closely schooling one. However, in many cases it is exceedingly difficult to determine whether a fish should be considered a closely aggregating form or a loosely schooling one. The mackerel imposes no such difficulties. It remains in dense schools throughout life, except for possible dispersal at night. It is difficult to think of an instance, at least among vertebrates, in which individuality is as completely lost as it is in a mackerel or herring school.

Parr (1927) subjected the mackerel school to critical theoretical analysis. Several interesting conclusions were reached which will be considered later. His report, however, contains relatively little experimental data. It is the purpose of this report to treat the phenomenon experimentally and, wherever possible, to attempt correlation with Parr's theoretical conclusions.

The writer wishes to express his deep appreciation to the U. S. Fish and Wildlife Service at whose Woods Hole station the experiments were performed; also to Dr. R. Buchsbaum whose photographic skill is responsible for the figures in the plate.

EXPERIMENTAL STUDY.

Number of Individuals Needed to Form a School: The experimental animals used in these and subsequent tests were 8-inch specimens of the chub mackerel, *Pneumatophorus grex* (Mitchill). Originally caught in the waters off Woods Hole, they were subsequently kept in appropriately large tanks in the laboratory. Several days were allowed for acclimatization before the animals were used. Two tanks were employed for experimental purposes. One was a rectangular assembled aquarium with transparent glass sides whose dimensions were 36″ by 15″ and 17″ deep. The other was a rectangular wooden tank 44″ by 23″ and 9.5″ deep. Sea water was kept running through these tanks at all times at a fairly rapid rate. The average oxygen content was 5.60 cc. per liter and the temperature range was 18–20 degrees C. In general, the mackerel survived well. Of those that died, many expired during the course of acclimatization in the laboratory. Most of those which survived this period lived for several weeks in no apparent distress.

Repeated experiments demonstrate that

two individuals suffice to form a mackerel school. If two fishes are removed from a group and placed in the wooden tank they immediately school, i.e., swim about the tank nearly always in line with each other. If one mackerel is kept isolated in a tank and another is grouped with it, they immediately school. Apparently, the fish that first becomes aware of the presence of the other initiates the schooling reaction. Whether this will be the original fish or the introduced one is purely a matter of chance for it will be one or the other 50% of the time. Other fishes added to this group of two immediately join the school.

Thus, only two individuals are required to begin the formation of a mackerel school which is, however, better integrated if composed of many individuals.

Breder & Nigrelli (1935) found that two sunfishes, *Lepomis auritus*, grouped together in a tank "aggregate" with each other after two days. Shlaifer (1938) demonstrated that the oxygen consumption and locomotor activity of an isolated goldfish is significantly higher than is that of an individual in a group of two.

It would seem, at least in the cases listed above, that there is a much greater psychic difference between an isolated fish and one in a group of two than between the latter and an individual in a much larger group.

Effect of Various Types of Blinding: Parr (1927) found that when chub mackerel were blinded by the application of vaseline and lampblack to the eye, they did not school or mill. Blinded catfishes do not aggregate (Bowen, 1931) nor do blinded sunfishes (Breder & Nigrelli, 1935). Grouped goldfishes which are normally less active than isolated individuals lose this group effect when they are blinded (Shlaifer, 1939). These results as well as other lines of evidence indicate the importance of vision in integrating social behavior in fishes.

The experiments described below were designed to repeat and to extend the original work of Parr (1927) on this species. Mackerel were blinded by piercing the cornea and were kept in the wooden tank described above. One day was allowed for recovery from operative shock. Blindness was ascertained by appropriate tests, e.g., failure to avoid a net, etc. All results noted for the various blinding experiments were confirmed by repeated tests. As controls, the area in the vicinity of the eye of nonblinded mackerel was pierced by the same instrument used for blinding, thus approximating similar conditions of shock. In no case did control individuals fail to school when grouped.

If an individual is blinded on one eye and subsequently grouped with six schooling mackerel, it immediately joins the school. In fact, if only three minutes are allowed for recovery from the shock of the operation instead of the customary day, it also rejoins the school immediately. This half-blinded fish succeeds in maintaining its orientation with respect to the rest of the school fairly well. Sudden turns by the normal animals to the blinded side of the experimental fish may result in temporary loss of integration of that animal with the school; however, it is quickly recovered.

If a mackerel is subjected to bilateral blinding, it makes no attempt to join the school. Occasionally its random movements about the tank may disrupt the smooth integration of the normal school but only for a moment.

The grouping of a normal fish with a half-blinded one results in a schooling reaction. In general, the unilaterally blinded animal will orient itself so that the intact eye side is the one nearest the normal fish. Sudden turns by either animal will initiate a turn in the other, thus maintaining the school. If the half-blinded fish is then blinded on the other eye, the school disintegrates. There is, of course, no reaction by the sightless form to the normal one. However, it might be expected, inasmuch as there is no other mackerel in the tank but the blinded individual, that the normal fish would attempt to school with it. This is not the case.

Sightless mackerel do not swim in a typically normal manner; movement is slower and less uniform. Apparently, normal swimming movement is of great importance in the schooling reaction of mackerel.

If two mackerel are blinded on the same eye, a school obtains though it is not as well integrated as is a school of two normal individuals or one normal and one half-blinded form. In this case the maintenance of the school is dependent upon the behavior of the fish whose intact eye side is nearest the other animal whose swimming movement is apparently sufficiently normal to evoke a schooling reaction by the mackerel which is in visual contact with it. We are presented with the unusual case of a school of two fishes, one of which plays a passive role. Sudden turns and changes in direction may reverse the role of either fish. The mackerel which sees the other member of the group of two usually follows the turns of the passive partner. On occasion, however, it may initiate a turn, in which case the school is broken for a second or so until one individual finds the other.

If, in a group of two, one mackerel is blinded on its left eye and the other on its right one, schooling behavior is very erratic. If their blinded sides face each other no reaction obtains; if not, they school, though the school is likely to be broken by a sudden sharp turn by one animal which results in

their blinded sides facing each other again.

A totally blinded fish grouped with a half-blinded one evokes no good schooling reaction by virtue of the abnormal movement of the former. Two totally blinded individuals grouped together will swim at random and may collide.

Confirming Parr's data (1927), three mackerel blinded in both eyes and placed in an exhibition tank containing a large school of mackerel swim aimlessly and make no attempt to join the group.

The results obtained demonstrate the role of vision. Also indicated is the importance of normal swimming movement.

Any experiment in which visual response is eliminated through blinding suffers from the criticism that the normal physiological state of the animal may be disturbed. This may be true even when a period deemed to be sufficient for recovery from shock obtains. A more natural condition is darkness and a description of the behavior of mackerel in this state follows.

The Effect of Darkness on Schooling: Newman (1876) finds that the closely schooling herring, *Clupea harengus*, break up completely at night in a tank in captivity, each fish taking an independent path. The school reforms in the presence of sufficient light. Breder (1929) reports that compact schools of *Jenkinsia*, also a member of the family Clupeidae, are dispersed at night. Bowen (1931) finds that aggregations of catfishes are dispersed in darkness. Breder & Nigrelli (1935) report that aggregations of the sunfish, *Lepomis auritus*, break up with the coming of night. Shlaifer (1939) finds that the effect of grouping (decreased oxygen consumption) on goldfishes disappears in total darkness.

The behavior of mackerel in darkness was investigated by two procedures, one observational, the other photographic. One of the exhibition tanks of the Aquarium at the Woods Hole station of the U. S. Fish and Wildlife Service contains a school of forty to fifty 8-inch chub mackerel, as well as a turtle, flounder, blackfish, and skate. The tank, rectangular in shape, is 6.5 feet by 4 feet and 3 feet deep. Three of the vertical sides are composed of stone and cement and the fourth of transparent glass.

The lights in the Aquarium were always off at night and after 9 p.m. the room was quite dark. The observer, looking at the tank from above or standing next to the transparent glass side, could see nothing in the tank; in fact, one's hand held two inches from the eye was quite invisible. For several hours at night during several consecutive evenings observations were made on the schooling behavior of the mackerel in this state of darkness. At half-hour intervals a flashlight beam was directed at the bottom of the exhibition tank for only one or two seconds. If maintained longer, the fishes would react to the light, weak though it was, by forming a dense school. Hence, it was necessary to form an impression of the aggregating condition of the group in this very short time. The general impression gathered by these observations was that the school was fairly well dispersed. The fishes were never found to be closely schooling or milling but neither were they swimming about the tank at random as Newman (1876) reported for the herring in darkness. The mackerel swam in an elliptical orbit more or less in the same direction but with considerably greater distances between individuals than is found in a normal school in the light. Considering the number of individuals, the size of the tank, and the tendency of mackerel to swim in a uniform way for hours unless disturbed, the observed state of the school is probably what is to be expected in the absence of visual integration. Further experiments are planned along these lines.

The mackerel eye is apparently capable of detecting similarly moving forms at very low light intensities for when they could just barely be seen they were in fairly compact schools. This is in contrast to the findings of Breder & Nigrelli (1935) for sunfish aggregations which break up when they can still be seen distinctly. Another interesting fact is that the mackerel also is capable, apparently, of seeing in light at the deep red end of the spectrum. When a Wratten Series II Safelight, which transmits light in the deep red from about 650$\mu\mu$. to 700$\mu\mu$., was suspended at night over the tank several inches from the water surface in otherwise total darkness, the mackerel formed fairly compact schools and mills. (See Plate I, Fig. 3.)

The observational method described above is open to the criticism that the observer's reaction must be instantaneous and is subjective. Accordingly, a series of flash-bulb photographs was made of the mackerel group in artificial light and in total darkness. These flash-bulb photographs are taken in a fraction of a second, much too fast for any disturbance caused by the blinding flash of light to be recorded in the photograph. The school was photographed from the side through the transparent glass. Darkness shots were taken only after a period of at least 15 consecutive minutes of darkness following the small amount of illumination from a flashlight incident to setting up the equipment. Darkness set in at about 9 p.m. and the first photograph was usually taken at about 10 p.m. Plate I contains two photographs which represent typical results. Fig. 1 is a compact mackerel school under fairly strong artificial light. Fig. 2 was taken in total darkness at about 10:30 p.m. The contrast in the denseness of the aggregations

is obvious and portrays the results obtained by observation.

The observational and photographic evidence reveals that mackerel schools apparently are dispersed in total darkness. However, the ability of mackerel in aquarium tanks to school at very low light intensities leaves unsolved the condition of mackerel schools in nature where dim light may obtain at night. It is the intention of the writer to pursue this matter more exhaustively in future work.

Visual Contact: Shlaifer (1939, 1940) found that the oxygen consumption and locomotor activity of isolated goldfishes in visual contact with others of the same species and variety was of the same order of magnitude as that of these individuals when actually members of a group. This confirmed previous results which demonstrated the visual integration of the group effect. Although darkness and blindness tests have indicated the importance of vision in the schooling behavior of mackerel, the following experiment was performed as a bit of additional evidence.

The glass tank whose dimensions have been listed above was divided in half along its length by a plate of transparent glass. One mackerel was placed on each side. After a short period of acclimatization, the two fishes tended to swim close to the dividing glass plate in line with each other. In general, the animals would turn only when they reached one end of the tank and would then swim back to the other end. If, however, one mackerel turned in the center of the tank, the fish on the other side of the glass in visual contact with it would usually also turn before reaching the end of the tank. This behavior was not invariable but occurred with sufficient frequency to be considered significant.

Thus, from three lines of evidence—blinding, darkness, and visual contact experiments—the important role of sight is demonstrated.

Response to Form and Movement: Spooner (1931), working with the bass, *Morone labrax*, which is a schooling form, found that individuals would be attracted to dead, mounted, specimens of the species but not to rough models. Similar results were obtained for the goldfish (Shlaifer, 1939, 1940). Thus, there is indicated that there may be a visual response to objects of the proper form though they are devoid of movement. Response to form is also reported by Breder (1929) for the schooling herring, *Jenkinsia*, and by Breder & Nigrelli (1935) for the aggregating sunfish, *Lepomis auritus*. On the other hand, many sexual behavior studies emphasize the importance of movement (Noble, 1934; Breder, 1936).

Experiments demonstrate that a mackerel isolated in a tank with freshly killed and mounted specimens placed in the normal swimming position, does not react to them. On the other hand, if another normal mackerel is introduced into the tank, the schooling reaction is immediately evoked.

Repeated experiments were performed with freshly killed mackerel which were manipulated by means of a long rod, the hooked end of which was inserted in the back of the fish. A normal mackerel was grouped with a mounted fish which was then manipulated so as to simulate a normal swimming animal. In only one case in 70 trials was there any response given to the dead specimen. Again, normal mackerel introduced into the experimental tank elicited immediate schooling. An olfactory basis for the lack of response to a dead, manipulated individual is not probable by virtue of the fact that the animals were freshly killed and were in fairly rapidly flowing water.

It may be concluded that normal swimming movement is an important factor in the schooling reaction. True, with normal movement a mackerel may be attracted by the body form of its neighbor but, in the absence of normal movement, form alone will not suffice. The importance of normal movement is further emphasized by the failure of a mackerel to school with a blinded individual which does not swim in the usual manner. Evidently, mackerel are sensitive to differences in motion which we can also detect and quite possibly to minor differences which we cannot observe. Nevertheless, further experimentation along these lines is in order. If simulation of swimming motion in a killed mackerel can be skillful enough to evoke a schooling reaction, neat checks might be obtained on response to form by altering in many ways the shape of the dead specimen.

Response to Color: The reaction of fishes to colors is still the subject of considerable debate. Warner (1931) criticized the lack of control of the intensity factor and deemed most of the experimental work worthy of repetition. White (1919, 1927) demonstrated that mudminnows and sticklebacks can discriminate between wave lengths and not merely intensities of light. Brown (1937) found that the large-mouthed black bass, *Huro salmoides*, responds to differences in wave lengths. Noble & Curtis (1939) demonstrated that young cichlids may be born with a greater interest in moving red discs than in moving black, blue, green or yellow ones.

Shlaifer (1939), though not differentiating between wave length and intensity, found that the group reaction in the goldfish was not in any way based on color differences or similarities. Accordingly, ex-

periments were performed with mackerel to determine whether response to color was in any way involved in the schooling behavior. Mackerel were removed from the tank and paints of various colors were applied over all of the body but the eye. They were then allowed a period of recovery from shock and were grouped in various combinations. Specimens painted blue were grouped with ones painted white, black, etc. In all cases, schooling occurred immediately with no indication whatsoever of differential response to color.

Effect of Isolation: Bowen (1932) found that the sight response of normal aggregating catfishes to one another was not completely eliminated in all individuals by 161 days of isolation. It was much less marked but was re-established in the course of a few minutes, usually after contact occurred. Catfishes isolated for only 52 days when grouped together showed no difference in behavior from those animals kept in a group.

Five mackerel were isolated for 20 days, the maximum time available before the laboratory closed. At the end of this period, two of the five were grouped together as were the remaining three. Schooling occurred immediately. If mature mackerel could be kept in isolation for much longer periods, it would be interesting to observe subsequent schooling behavior. Even more interesting would be the subsequent schooling reaction of mackerel reared in isolation from various early stages.

Discussion.

The experimental results reported above confirm the data of Parr (1927) on the visual integration of the mackerel school. Further, it is seen that only two normal individuals are necessary to begin a school. The visual response is apparently not correlated with color but is with normal swimming activity. Finally, several weeks of isolation do not induce any weakening of the schooling reaction.

The fact that two individuals suffice to begin a school, at least under laboratory conditions, may have implications for larger aggregations in nature. If schools are completely dispersed at night, their reformation in daylight would be definitely facilitated by the mutual attraction of only two fishes. In fact, again granting the break up of the school at night, without a schooling response by one solitary fish to another one, it is difficult to see how schools could reform.

In reference to the apparent visual integration of fish schools, Parr (1927) indicates that schooling pelagic fishes have eyes of large size and rather scantily equipped lateral line systems. He concedes that lateral line stimuli might come into play once the mackerel, by visual stimuli, approached each other. However, his data and those reported above on the behavior of blinded fishes would not tend to confirm this hypothesis.

Parr attributes the schooling reaction of mackerel to a simple automatic eye reflex rather than to a social instinct involving the entire school. The apparently senseless milling reaction is caused, he believes, when the school as a whole tries to make a turn of more than 180 degrees and is thus turned back on itself. This behavior pattern tends to emphasize the rather mechanical nature of the school.

Since the reaction of a mackerel to others of its kind is not to color it must be to form. However, form alone will not induce the schooling act if swimming movement is not normal. The fact that mackerel are evidently capable of detecting slight differences in movement would put the reaction of the fish on a slightly higher plane. Extensive heterotypic grouping experiments are planned which would tend to shed much light on the factors of response to various types of body form and movement. Further interesting data might be obtained by observing the reaction by an isolated mackerel to its mirror image. Following the work of Spooner (1931), the reflecting surface of the mirror could be broken by lengths of tape at definite intervals; in this way the reaction of the animal to body form which is identical with its own but not complete might be ascertained.

The condition of various types of fish schools and aggregations is summarized in a schematic diagram by Breder & Nigrelli (1935). Compared with other fishes possessing social tendencies, the schooling of mackerel is striking by virtue of its fixity. Nevertheless, the survival value of this mechanically highly integrated group is still not clear.

An interesting feature of the mackerel school is the spacing of the individuals in the group. The distance between the animals is more or less constant. A school may be greatly concentrated, however, by a sudden disturbance which produces a "fright" reaction — after being momentarily dispersed the fishes rush together in a compact mass which soon, however, returns to normal proportions. Parr (1927) states that when the fishes in a closely schooling group approach each other too closely, their images may become too large and the accompanying strenuous accommodation of the eyes may produce a negative response, thus regulating the spacing. Breder (1929) states the proposition that such fishes that depend on visual reactions for the formation of schools approach no closer to other objects than that distance at which they become clearly visible. This problem may be approached experimentally.

Whether the schooling habit is ontogenetically or phylogenetically acquired and whether the schooling or solitary state is the primitive one are important theoretical considerations. It is to be hoped that future investigation will shed some light on these problems.

Summary.

1. Although larger groups are better integrated, two individuals suffice to begin the formation of a mackerel school.

2. Blinding, darkness, and visual contact experiments indicate that the schooling reaction of the mackerel is visually integrated.

3. Mackerel display no schooling reaction to others of the same species, living or dead, which move or are moved in a manner not completely normal.

4. As far as tested, response to body color plays no role in the schooling reaction.

5. Isolation for three weeks does not eliminate or reduce the schooling proclivity.

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EXPLANATION OF THE PLATE.

Plate I.

Fig. 1. A school of chub mackerel, *Pneumatophorus grex*, in an exhibition tank under fairly strong artificial light.

Fig. 2. A flash-bulb photograph of the same school in total darkness—dispersed.

Fig. 3. Mackerel milling in light in the deep red—650 μμ to 700 μμ.

(The photographs include the upper four-fifths of the vertical depth and the central four-fifths of the length of the tank).

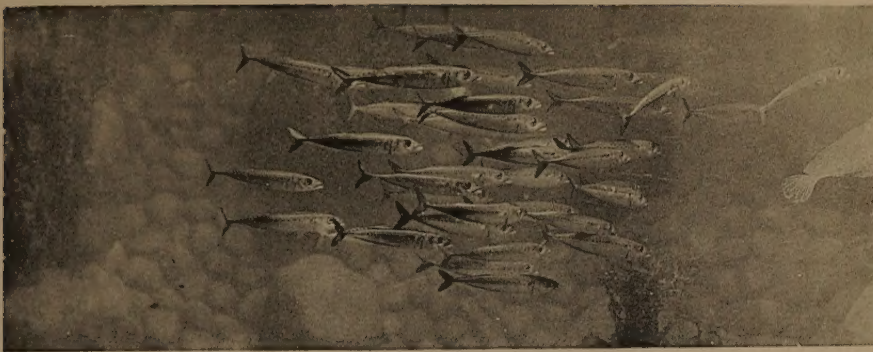

FIG. 1.

FIG. 2.

FIG. 3.

THE SCHOOLING BEHAVIOR OF MACKEREL: A PRELIMINARY EXPERIMENTAL ANALYSIS.